Taxonomy and classification: conceptual history

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What is a classification?

In classifying organisms, biologists sort them out into categories and label each category with a noun. The categories are called *taxa* (singular *taxon*) and the noun labels are called *nomina* (singular *nomen*). *Systematics* is the theoretical study of how taxa should be drawn up; *taxonomy* is the practical discipline concerned with the giving of nomina to taxa.

There are two main sorts of nouns. *Common* nouns (e.g., "diamond" or "predator") delimit sets defined by essential descriptive properties. The essence of a diamond is to be composed of carbon atoms arranged in a certain way; the essence of being a predator is killing and eating animals. By contrast, *proper* nouns (e.g., "Italy" or "Caligula") refer to single, unique individuals defined by temporal, spatial, and causal continuities, not by essential properties. (The newborn Caligula had nothing particular in common with the assassinated emperor.) Vernacular nouns that denote categories of organisms (e.g., "horse," "worm," "predator") are common nouns. In some approaches to systematics, taxon nomina are likewise common nouns. In others, which are currently more prevalent, nomina are proper nouns—names of sets, in the same way that "Caligula" is the name of a unique individual.

The members of a species share certain statistically normal properties, which allow them to recognize each other as potential mates and interbreed. However, these are not properties of the species. (Horses typically have four legs, but the horse species *Equus caballus* has no legs at all.) Most systematists would say that these are not even essential properties of the species' members, because they can vary within the species, and usually do. (People typically have big brains, but small-brained people are still members of our species.) Biologists today generally regard a species as a logical individual, delimited by the property of historical continuity (through past and potential reproduction), rather than by any set of directly observable essential traits.

However, *identifying* an organism as a member of a particular species rests on diagnostic observable traits. "Classification" therefore comprises two different sorts of activity: (1) drawing boundaries that establish what species or other taxa are to be recognized (determining what things there are in principle); and (2) pigeonholing individual specimens into these species on the basis of their observed traits (telling things apart in practice). The tension between these two kinds of activities has pervaded the history of biological classification.

Linnaean essentialism

Some of this tension can be traced back to the Swedish naturalist Carl Linnaeus (1707–78), who established the system of zoological classification and naming used today. Taxa and nomina proposed in the canonical 10th (1758–59) edition of Linnaeus's *Systema Naturae* (*System of Nature*) include many that are still recognized, including our own class (Mammalia), order (Primates), genus (*Homo*), and species (*Homo sapiens*). Linnaeus's system differed in three important respects from previous attempts to catalog and organize the diversity of living things:

- His system was *universal*, comprising all natural objects and capable of infinite expansion to encompass new discoveries.
- His system was organized into a *logical hierarchy*. Ancient and scholastic logicians liked to organize concepts into nested sets, with general categories (L. *genera*, singular *genus*) encompassing more specific ones (L. *species*, singular *species*). Thus, the genus "polygon"

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contained innumerable species (triangles, quadrilaterals, pentagons, etc.), while the genus “triangle” contained three species (right, acute, obtuse). Linnaeus imposed this system on animals and plants, setting up hierarchical levels of taxa in which generic terms at one level became specific terms at the next highest level. He labeled these ranked categories, in ascending order of inclusiveness, the *genus* (a set containing one or more species), *order*, *class*, and *kingdom*. Later workers, making increasingly fine subdivisions to accommodate millions of species, have had to add additional levels, with multiple super-, sub-, and infra-levels at each rank (see PRIMATE TAXONOMY).

- Linnaeus aimed at producing a *natural classification*. He believed that God had created higher-order taxa as well as species, and he aimed at identifying the properties essential to those taxa. What this meant in practice can be seen by comparing successive editions of the *Systema Naturae*. In the first (1735) edition, Linnaeus identified the skin and limbs as the essential characters defining vertebrate classes. He therefore placed the whales and sea cows in the class of fish (Pisces), defined by having no feet and a naked body. The rest of the mammals went into a class Quadrupedia, whose essential characters were four feet, hair, live birth, and lactation. By the time of the 10th edition, he had concluded that lactation was more expressive of the milky, maternal mammalian essence than hair and legs. He therefore moved the marine mammals into the Quadrupedia and gave the new grouping its current milk-based name, Mammalia. Because the nomina in his system were defined by essential properties, they were logically common nouns.

Two sorts of objection to Linnaeus’s approach were voiced. The French naturalist Michel Adanson (1727–1806) argued that the characters used to define taxa should be those with the greatest number of correlates. Adanson’s anti-essentialist systematics went largely unnoticed until the twentieth century. A more influential opponent was Georges-Louis Leclerc, Le Comte de Buffon (1707–88), who rejected the possibility of systematic classification. Nature, wrote Buffon, “passes from species to species and often from genus to genus by imperceptible gradations … which necessarily throw into disarray the prospect of any general system” (Buffon and Daubenton 1766, 13).

Linnaeus’s system prevailed despite Buffon’s objections, because biological discourse demanded some sort of systematic terminology. For a century after Linnaeus, zoologists strove to refine his system by recognizing natural-seeming groups of animals and then trying to pick out essential properties that would generate the observed order. Each set of properties that was proposed yielded sporadically useful organizing principles; but none was generally applicable, and there were no theoretical grounds for preferring one to another.

Darwin and classification

The enterprise of classification and its meaning were transformed by Charles Darwin (see DARWIN, CHARLES R.). In *On the Origin of Species* (1859), Darwin wrote, “Naturalists try to arrange the species, genera, and families in each class, on what is called the Natural System. But what is meant by this system?” (p. 413). Rejecting previous attempts to pick out key characters—in reproductive organs, ecology, embryonic development, body plan, etc.—that could generate a natural classification, Darwin argued that the nested sets of the Linnaean system were natural only insofar as they corresponded to the temporally successive branchings of an evolutionary tree. Whales are to be classified with sheep rather than sharks because they have more recent common ancestors with sheep. “Propinquity of descent,” Darwin concluded, “the only known cause of the similarity of organic beings, is the bond, hidden as it is by various degrees of modification, which is partially revealed to us by our classifications” (Darwin 1859, 414). With characteristic deep insight, Darwin saw that taxa defined by commonality of descent need not have any defining properties at all: “Let two forms have not a single character in common, yet if these extreme forms are connected together by a chain of intermediate groups, we may at once infer their community of descent, and we put them all into the same class" (Darwin 1859, 426).

In Darwin's view, the distinct gaps between taxa were largely an illusion, produced by the extinction of intermediate forms and the imperfection of the fossil record. Darwin wrote, "We may thus account even for the distinctness of whole classes from each other—for instance, of birds from all other vertebrate animals—by the belief that many ancient forms of life have been utterly lost, through which the early progenitors of birds were formerly connected with the early progenitors of the other vertebrate classes" (Darwin 1859, 431). Two years after these words were published, Darwin's expectation was verified when fossils of *Archaeopteryx*, a small dinosaur-like primitive bird with teeth and a long bony tail, came to light in Germany. From this point on, systematics began to have a predictive aspect grounded in biological theory.

Evolutionary systematics

We have noted three different ways of generating a Linnaean classification, differing in whether the concentrically nested taxa are defined (1) by a few essential properties (Linnaeus's approach), (2) by summed properties (Adanson's proposal), or (3) by genealogy only (Darwin's suggestion). For more than a century following Darwin's *On the Origin of Species*, a fourth, mixed system prevailed, in which both genealogy and overall properties were taken into account.

This approach can be illustrated with reference to the relationships and classification of birds. It was clear from the 1860s on that in many ways birds were more like reptiles than like mammals, and that they particularly resembled small theropod dinosaurs. These resemblances were at first thought to be primitive retentions from ancestral reptiles in the Paleozoic (Switek 2010). However, subsequent research and discoveries established that birds share special, nonprimitive features with the "archosaur" group of reptiles (including dinosaurs and crocodiles). By the 1930s, it was generally agreed that birds are more closely related to archosaurs than to other Reptilia (turtles, lizards, snakes, pterosaurs, etc.). Still, that was not regarded as a reason for moving birds into the class Reptilia as archosaurs, or for reclassifying dinosaurs and crocodiles as birds (class Aves). Birds were felt to be so different—*essentially* different—from those scaly, cold-blooded creatures that classifying birds with dinosaurs to the exclusion of lizards and turtles would produce groupings with little descriptive content or biological meaning.

The mixed system that resulted attempted to accommodate descriptive criteria of classification as well as genealogy. In this system, known as *evolutionary systematics*, a Linnaean taxonomy is generated by drawing nested taxon boundaries as closed curves bounding portions of the evolutionary tree diagram (Figure 1a,b). Wherever the curve cuts through the tree, it produces a *grade boundary* separating an ancestral group below the cut from a descendant group above it. The ancestral group retains primitive features lost or modified in the descendant group. It may include later-surviving branches of the tree that have remained persistently primitive in those features—for example, the class Reptilia excluding birds (Figure 1 in MONOPHYLY), or the ape family Pongidae excluding humans and their bipedal ancestors and relatives (Figure 1).

In the canonical mid-twentieth century version of evolutionary systematics (Simpson 1961; Van Valen 1971; see SIMPSON, GEORGE GAYLORD), grade boundaries were drawn to coincide with major changes in adaptation, such as the transition to flight that distinguished the ancestral birds from their dinosaur ancestors, or the shift to life on the ground that distinguished the ancestral hominids from their arboreal ancestors. Drawing boundaries in this way ensures that each taxon will be defined by biologically significant traits of evolutionary importance. The use of grade boundaries also allows the persistently primitive groupings to function as so-called *wastebasket taxa* (e.g., Reptilia), into which early and unspecialized members of a larger grouping can be dumped without worrying about their precise genealogical relationships. Because each taxon in an evolutionary classification is a specifically delimited part of the evolutionary tree, each is a logical individual and its nomen is a proper noun.

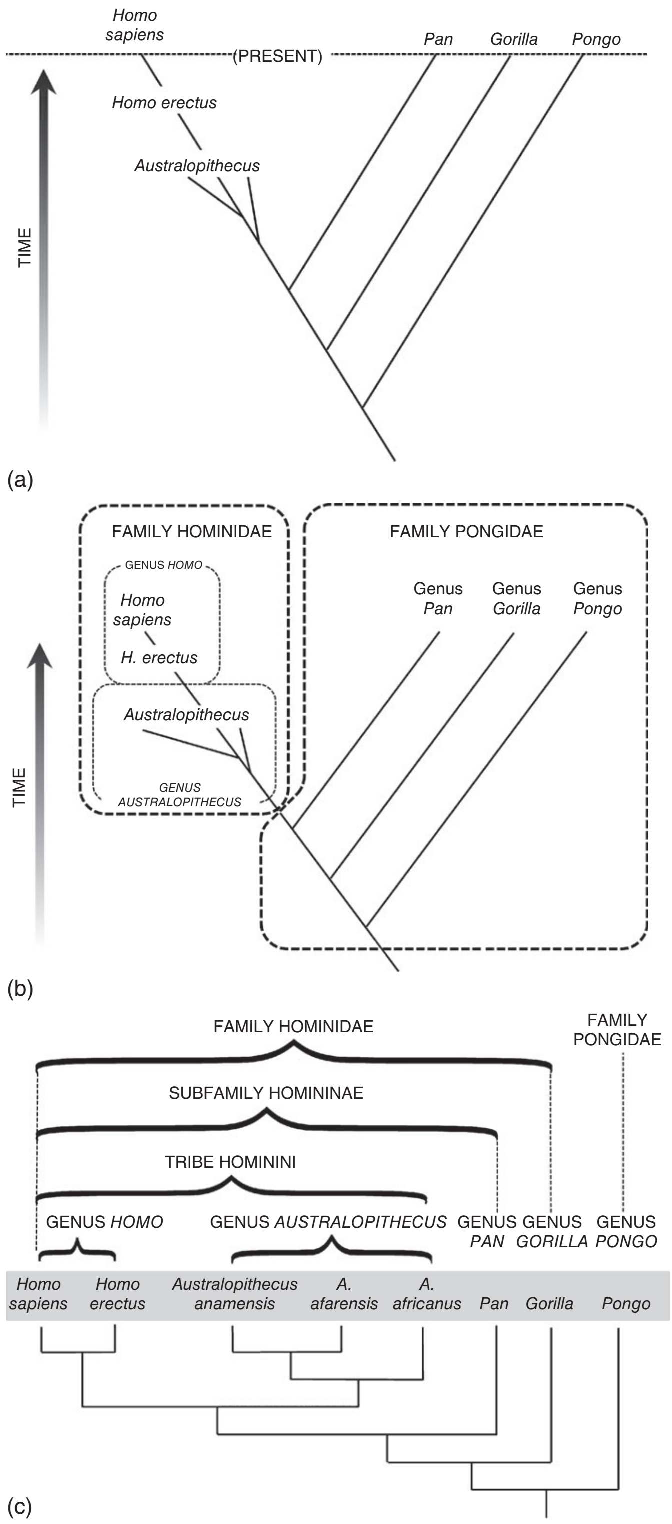
Homo sapiens
(PRESENT)
Pan
Gorilla
Pongo
Homo erectus
Australopithecus
TIME
(a)
FAMILY HOMINIDAE
FAMILY PONGIDAE
GENUS HOMO
Homo sapiens
H. erectus
Australopithecus
GENUS AUSTRALOPITHECUS
Genus Pan
Genus Gorilla
Genus Pongo
TIME
(b)
FAMILY HOMINIDAE
FAMILY PONGIDAE
SUBFAMILY HOMININAE
TRIBE HOMININI
GENUS HOMO
GENUS AUSTRALOPITHECUS
GENUS PAN
GENUS GORILLA
GENUS PONGO
Homo sapiens
Homo erectus
Australopithecus anamensis
A. afarensis
A. africanus
Pan
Gorilla
Pongo
(c)

Figure 1 Evolutionary versus phylogenetic classification. (a) Evolutionary tree diagram (*phylogram*) with a time axis (not to scale), showing how the human species *Homo sapiens* is genealogically and temporally related to some of its ancestors and collateral relatives. (b) Evolutionary classification draws taxonomic boundaries directly on the phylogram, producing grade boundaries between ancestral (primitive) and descendant (derived or specialized) groups. Grade boundaries are positioned to coincide with major changes in adaptation—here, between arboreal apes (pongids) and terrestrial bipeds (hominids), and between *Australopithecus* and *Homo.* Ancestral groupings below each grade boundary (Pongidae, *Australopithecus*) constitute paraphyletic or *wastebasket* taxa. Such groupings may include relatively primitive forms surviving later in time (e.g., *Pan*, *Gorilla*, and *Pongo*). (c) Phylogenetic (cladistic) classification has no time dimension. All forms being classified are placed on the same line (gray band) and connected by a branching tree showing their phylogenetic relationships, with suspected ancestor–descendant pairs (e.g., *Homo erectus* and *H. sapiens*) represented either as conspecific (a single species) or as nearest relatives (sister groups). The resulting atemporal tree diagram (*cladogram*) is then read out as a Linnaean classification by translating successive branchings into nested sets (brackets at top). All taxa are clades, and there are no grade boundaries. As a result, many taxa (e.g., Hominidae) have no distinctive adaptations or morphologies. A complete phylogenetic classification of this part of the tree of life would include more species and more levels of branching, and would therefore use additional levels of the Linnaean hierarchy (super- and subgenera and tribes, superspecies, etc.).

Numerical taxonomy

Drawing horizontal grade boundaries involves subjective judgments. For example, we now believe that many flightless dinosaur relatives of *Archaeopteryx* had warm blood and feathers. Should they be called birds for that reason, or is flight the crucial adaptive shift that defines birds? Dissatisfaction with the subjective aspects of evolutionary systematics led in the 1960s to the revival of an Adansonian approach to classification. In this approach, the organisms being classified are analyzed into a series of *characters*, each with two or more states that differ among them. An example of a character might be "number of fingers on each hand," with states ranging from "five" (humans) to "one" (horses). Computer algorithms are then used to group the character-state data into Linnaean nested sets—taxa—that maximize the number of shared character states in each set. P. H. A. Sneath and R. R. Sokal (1962), the chief proponents of this so-called *numerical taxonomy*, insisted that "taxonomic relationships are to be evaluated purely on the basis of the resemblance existing in the material at hand," and that phylogeny should play no role in classification. By these rules, taxa are defined entirely by descriptive properties (Sneath and Sokal 1962, 857), and so their nomina are common nouns like "predator."

Phylogenetic systematics

During the 1950s, the German entomologist Willi Hennig developed a theory of systematics based on exactly the opposite assumption: that classification should be based exclusively on phylogenetic (see PHYLOGENETICS) relationships. Hennig insisted that all taxa be *clades* (see CLADE), meaning groupings containing all and only the descendants of their last common ancestor. It follows logically that there can be no horizontal grade boundaries separating ancestors from descendants. All taxonomic boundaries must be drawn vertically through nodes or furcation points on the tree diagram, converted here into a *cladogram* (see CLADOGRAM)—an abstract phylogeny lacking a time dimension (Figure 1c). Each taxon must therefore be the *sister group* of another taxon of the same rank, deriving from the other branch at the ancestral node. The classification simply maps the cladogram. As in evolutionary systematics, taxa are individuals and their nomina are proper nouns; but wastebasket taxa defined by relatively primitive character states are not allowed, as they are in evolutionary systematics.

In other hands, phylogenetic systematics soon incorporated the quantitative and computational methods of numerical taxonomists, some of whom insisted that it was something they had in mind all along (Sneath 1995). In its computerized form, sometimes called *cladistics*, it has become nearly universal as the standard approach to animal classification (Wiley and Lieberman 2011). Yet despite claims to the contrary, it retains arbitrary and subjective elements, because different but equally justifiable definitions and weightings of characters and their states can yield different cladograms. Forbidding wastebasket taxa also means that the traits defining higher taxa gradually converge on trivial, species-level differences as more is learned about organisms and their ancestors (Cartmill 2012). Because evolutionary and phylogenetic systematics each has its own merits and defects, both are still practiced (see HOMINOIDEA: CONCEPTUAL HISTORY and PRIMATE TAXONOMY), arguments between their proponents persist, and mixtures of the two are sometimes encountered.

Because the diversity of life has been generated in a messy, gradualistic, Darwinian fashion, a wholly satisfactory system of cutting it up into sharply defined sets and subsets may be unattainable. The closest we can come in theory to the natural system that Linnaeus sought is probably the strictly genealogical arrangements of cladistic systematics. Nevertheless, as Darwin foresaw, what seems sound in theory is not always practically useful in capturing an organism's important biological properties.

SEE ALSO: Nomenclature: usage; Synapomorphy

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